



Mites and ticks (Acari) Chapter 7.4

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Abstract

The inventory of the alien Acari of Europe includes 96 species alien to Europe and 5 cryptogenic species. Among the alien species, 87 are mites and 9 tick species. Besides ticks which are obligate ectoparasites, 14 mite species belong to the parasitic/predator regime. Among these species, some invaded Europe with rodents (8 spp.) and others are parasitic to birds (2 spp). The remaining 77 mite species are all phytophagous and among these 40% belong to the Eriophyidae (37 spp.) and 29% to the Tetranychidae (27 spp.) families. These two families include the most significant agricultural pest. The rate of introductions has exponentially increased within the 20th century, the amplification of plant trade and agricultural commodities movements being the major invasion pathways. Most of the alien mite species (52%) are from North America, Asia (25%), and Central and South America (10%). Half of the ticks (4 spp.) alien to Europe originated from Africa. Most of the mite species are inconspicuous and data regarding invasive species and distribution range is only partially available. More research is needed for a better understanding of the ecological and economic effects of introduced Acari.

Keywords

Europe, alien, mite, tick, Acari, Eriophyidae, Tetranychidae, biological control, *Tetranychus evansi*, *Oligonychus perseae*, *Polyphagotarsonemus latus*, *Brevipalpus californicus*, *Aceria sheldoni*, *Aculops pelekassi*, *Dermatophagoides evansi*, *Varroa destructor*

7.4.1. Introduction

The subclass Acari, which includes mites and ticks, forms an important part of the class Arachnida, with a worldwide distribution and with over 55,000 (Krantz and Walter 2009) species described to date. An estimate of up to half a million to a million more species await discovery (Krantz and Walter 2009). Mites and ticks are a very diverse group ranging in size from about 0.08 mm up to 1 centimetre long. Acari differ from others Arachnida by the fusion of the abdominal segments as in Araneae (spiders) and from spiders by the presence of a gnathosoma containing mouthparts, the fusion of the posterior part of the prosoma (the podosoma, bearing legs) and fusion of an opisthosoma into an idiosoma (Evans et al. 1996). Most species are free living and have different trophic modes, including phytophagous, predators feeding on a variety of small invertebrates, fungivores and detritivores. Some species have developed complex parasitic relationships with both vertebrate and invertebrate animals. A number of acarine groups are injurious to crops and to livestock, both because of their feeding activities and because of their capacity as vectors for a variety of disease organisms to their plant or animal host. While the Oribatida is an important group (more than 6,000 species) having a key role in soil equilibrium, data regarding invasive species and distribution range remain largely unavailable. Ticks are very peculiar acarines, since they are obligate ectoparasites. In this sense they form a very homogenous group, with the order Ixodida composed of only three families. In this chapter, the two groups of Acari, mites and ticks, will be treated separately. The ticks will be presented through the description of a few significant case studies. By contrast, mites being much diversified in their biology and habitat use, and being truly ubiquitous, will be presented systematically.

Mites have successfully colonized nearly every known terrestrial, marine, and freshwater habitat. The most studied and observed invaders are found among the phytophagous mites of the families Tetranychidae and Eriophyidae, which include important agricultural pests. There is a growing awareness of the economic relevance of eriophyids as crop pests, including their importance as vectors of plant viruses, their role as alternative food for predators of plant pests, and their potential as weed control agents (Sabelis and Bruin 1996). A description on spider mite biology and their control is presented in the extensive review by Helle and Sabelis (1985). In addition to plant-feeding mites, a second group includes the alien parasitic mites. Among them, some invaded Europe with rodents such as muskrats (six alien species of mites), and brown rats (two aliens), while others are bird parasites (two species). *Dermatophagoides evansi* (Pyroglyphidae) is not associated with rodents and it has probably been accidentally introduced by humans (Bigliocchi and Maroli 1995, Hughes 1976, Thind and Clarke 2001). A single species in the family Varroidae, *Varroa destructor*, is alien to Europe (De Rycke et al. 2002, Griffiths and Bowman 1981).

Ticks are important parasites of livestock, wild animals, and humans. After their parasitic phase, they spend most of their life cycle outside their hosts, where prevailing climate conditions may constrain their ability to colonize a given territory. While

some tick species are highly restricted to particular combinations of climatic variables, or have defined host species, others may occur in widely variable climate conditions and have catholic feeding habits. Some species of ticks can be considered as invasive species, since the uncontrolled movements of domestic animals may introduce alien species into Europe or disperse some species outside their native distribution ranges. The introduction via large-bodied host vectors (such as passerine birds) and the uncontrolled importation of reptiles, are important means for colonizing newly available areas. Furthermore, one species of tick, *Rhipicephalus sanguineus*, is spreading in parts of Europe out of its current range because of the movements of domestic dogs.

7.4.2 Taxonomy of the mite species alien to Europe

A total of 101 mite species have been considered as alien to Europe, including 96 species shown to have originated from other continents and 5 cryptogenic species (Table 7.4.1). These species involve 16 different families of mites (Figure 7.4.1). In addition, Table 7.4.2 provides some examples of mite species alien *in* Europe; i.e., European species introduced from one part of Europe to another where they are not native.

Alien mites belong to two super orders, **Acariformes (Actinotrichida)** and **Parasitiformes (Anactinotrichida)**. Most of these species belong to two orders of Acariformes, **Prostigmata** and **Astigmata**. Prostigmata includes the three most important superfamilies:

- * Tetranychoidea comprises two main families containing alien mites. The Tetranychidae family, or spider mites, includes 1,250 described species (http://www1. montpellier.inra.fr/CBGP/spmweb/). Among them, 100 can be considered as pests and 10 as major pests of agricultural crops. All stages are phytophagous and feed on parenchyma cells. No viruses associated with spider mites have been observed. The most widely distributed species is the highly polyphagous and ubiquitous *Tetranychus urticae* (two spotted spider mite), found on nearly 1,000 plant species. In Europe, alien spider mites are generally more specialized and occur on a single genus or family of plants. Due to their minute size (200 to 900 μ m) typical of many species of Acari, spider mites remain undetected until major plant damage occurs. The members of another family, Tenuipalpidae, or false spider mites, are important obligate phytophagous mites. They are elongate, dorsoventrally flattened and usually have a reddish colour.
 - * Eriophyoidea includes three families:
- Eriophyidae, to which belong ca. 88% of all known Eriophyoidea in the fauna of Europe (Fauna Europaea 2009). These are vermiform, four legged mites. The family includes important economic pests of broadleaved plants. All known mite vectors of plant pathogens and nearly all gall-forming species belong to this family. About half are vagrants. Most of the species in the genera *Aceria* and *Eriophyes* cause specific galls on the leaves, green twig, flower buds, vegetative buds, or fruit of the hosts (Oldfield 1996). Others, especially *Epitrimerus*, *Phyllocoptes*, *Aculops* and *Aculus* cause discolouration and other non-distortive damage to their hosts.

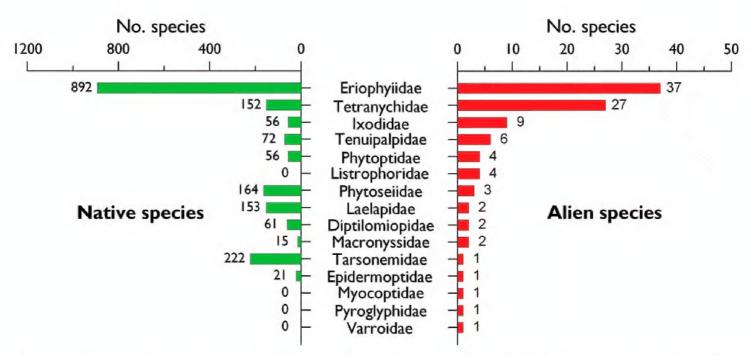


Figure 7.4.1. Relative importance of the mite families in the alien and native fauna in Europe. Families are presented in a decreasing order based on the number of alien species. Species alien *to* Europe include cryptogenic species. Only the most important families of native species (> 50 spp.) have been considered. The number over each bar indicates the number of species observed per family.

- Phytoptidae, which are obligate phytophagous and gall mites, with a high degree of specificity. They are also vermiform and four-legged. The family Phytoptidae is well represented on conifers (half of the described phytoptid species) and monocots. Phytoptidae is less represented than Eriophyidae or Diptilomiopidae on dicotyledons. Four alien species out of a total of 56 species have been reported in the fauna of Europe.
- Diptilomiopidae, which are predominantly leaf vagrants, only inhabiting leaves of dicotyledons, and rarely causing notable damage to their hosts (Keifer 1975). Two monotypic genera are known from only two families of monocotyledons (Poaceae and Palmae) occurring in the tropics. *Rhyncaphytoptus* species are mainly represented on several families of deciduous trees in the Holarctic region. Two alien species have been reported, out of the total 61 in the European fauna.
- * **Tarsonemoidea** represented by the family Tarsonemidae includes economically important mites. Most of them are mycophagous. Some species are phytophagous, whereas others are parasites of bark beetle eggs, or predators of tetranychid eggs. The most redoubtable pest species in the family is the broad mite, *Polyphagotarsonemus latus* (=*Hemitarsonemus latus*), which was described in 1890 and has recently been redefined and considered as being a species complex (Gerson 1992).

The order **Astigmata** is less represented in the alien fauna. A few species belong to the super-family **Sarcoptoidea**, and especially to families Listrophoridae and Myocopidae. Members of Listrophoridae are usually small, elongate mites and are skin or hair parasites of mammals. The palpae and/or legs I-II are often highly modified for grasping hairs. Four species of Listrophoridae mites have invaded Europe, grasped to the fur of muskrats: *Listrophorus americanus*, *L. dozieri*, *L. faini* and *L. validus* (Šefrová and Laštůvka 2005). Myocopids, or hair mites, live on skin of marsupial and rodents (Bauer and Whitaker 1981, Šefrová and Laštůvka 2005,

Whitaker 2007). *Myocoptes ondatrae* is an ectoparasite that has invaded Europe by grasping the fur of muskrats (Bauer and Whitaker 1981, Šefrová and Laštůvka 2005, Whitaker 2007). Other species belong to the super-family **Acaroidea** and families Epidermoptidae and Pyroglyphidae. Epidermoptidae are skin parasites of birds. *Epidermoptes bilobatus* causes avian scabies. Pyroglyphidae are external parasites living on bird feathers or are nidicolous. *Dermatophagoides evansi* feeds on human detritus, and lives in house dust as well as within bird nests (Piotrowski 1990, Razowski 1997).

Among the super-order Parasitiformes (Anactinotrichida), aliens belong to orders Ixodida and Mesostigmata. Ixodida is represented by the species in the family Ixodidae, which is treated in a separate section at the end of the chapter. Alien Mesostigmata belong to superfamilies Ascoidea and Dermanyssoidea. The first superfamily is represented by a single family with aliens, Phytoseiidae, which are predators of spider mites. In Europe, species such as *Phytoseiulus persimilis*, *Amblyseius* (*Neoseiulus*) californicus and Iphesius (Amblyseius) degenerans are used as biological control agents against phytophagous pests (Bartlett 1992, Croft et al. 1998, Easterbrook 1996, EPPO 2002, Garcia Mari and Gonzalez-Zamora 1999, Helle and Sabelis 1985, McMurtry and Croft 1997). Three families of Dermanyssoidea contain alien species. Varroidae mites are ectoparasites of honeybees. Varroa destructor is at present the most important parasite of Apis mellifera (L.). Varroa feeds on the haemolymph of adult, larval and pupal bees. Laelapidae mites live in soil, are nidicoles or parasitize small mammals and insects. Ondatralaelaps multispinosus is an ectoparasite of muskrats (Sefrová and Laštůvka 2005). Laelaps echidninus is a common worldwide ectoparasite of spiny rats, wild brown rats and is occasionally found on the house mouse and cotton rat (Wharton and Hansell 1957). Macronyssidae mites are haematophagous, have a large dorsal shield, prominent chelicerae and inconspicuous body setae (Easterbrook et al. 2008). Ornithonyssus bacoti is a parasite of rats, living in rat nests and their surroundings (Cole et al. 2005, Easterbrook et al. 2008, Fan and Petit 1998, Whitaker 2007). Ornithonyssus bursa is a natural parasite of common birds including pigeons, starlings, sparrows, Indian mynahs, poultry, and some wild birds, such as the robin (Berggren 2005).

7.4.3 Temporal trends of introduction in Europe of alien mite species

The rate of arrival of alien mites in Europe is increasing exponentially (Figure 7.4.2). An average of 2.1 alien species was newly recorded per year in Europe during 2000–2007 whereas only half this number was recorded during the period 1950–1974 (1 species/year). However, large differences were found between families.

The first records for Europe of all alien Tetranychidae are extensively documented in this chapter. There are no records reported before 1950; however, only few taxonomists were specialized on the family before this date. Since the second half of the 20th century, tetranychid species have been reported at an average rate of one new species every two years, with an acceleration of reports (one species per year) since 2000.

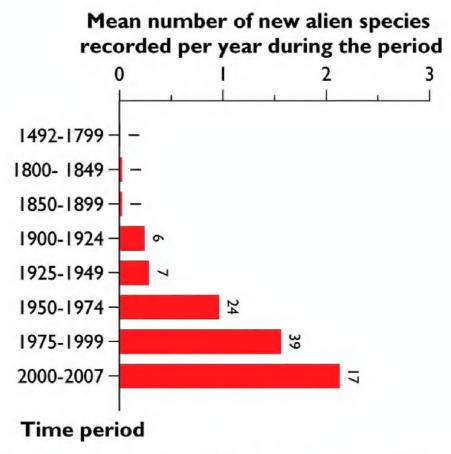


Figure 7.4.2. Temporal changes in the mean number of records per year of mite species alien *to* Europe from 1800 to 2009. The number over each bar indicates the absolute number of species newly recorded per time period.

Most of these mites represent agricultural pests, and therefore have been widely studied which explains the overrepresentation of crop pest species as Tetranychidae aliens.

The mean number of records of Eriophyoidae species alien to Europe increased rapidly during the third quarter of the 20th century. Only one species *Aceria alpestris*, which is alien in Europe, was recorded within the period 1850–1899. This species was described from the host plant *Rhododendron ferrugineum* L. from Tirol (Austria). The species was later recorded in mainland Italy, Czech Republic, Slovenia and Serbia, but it is not clear if it was associated with cultivated Rhododendron. Species recorded intensively between 1900–1924 (although described from Germany in 1857) are categorized as cryptogenic (Eriophyes pyri, the pear blister mite) or alien in Europe, like Aculus hippocastani (recorded in 1907, but probably introduced in Europe from the 17th century when its host plant Aesculus hippocastanum L. was intensively cultivated), and Aceria loewi (probably introduced in the 16th century when lilac started to be cultivated in France). Aculops allotrichus, which is alien to Europe, was recorded in 1912 but was probably, introduced with its host Robinia pseudoacacia L. which was for the first time introduced into France at the beginning of 17th century. Aceria erinea and A. tristriata were suspected to have an Asian origin and have been designated as aliens. They were recorded on 1903, but probably were present on its host, Persian walnut, in the Balkans and South Europe much earlier. Only one species in the Eriophyoidae was recorded between 1925–1949, e.g. Aceria petanovicae, the lilac rust mite. Being for long time known under the name of Aculops massalongoi the species is alien in Europe.

Six alien species to Europe were recorded between 1950–1974. Two pests of citrus, Aceria sheldoni (citrus bud mite) and Aculops pelekassi (citrus rust mite) and the azalea mite Phyllocoptes azaleae, are suspected to have been introduced from Asia. Characteristic symptoms of deformed lemon fruits caused by A. sheldoni were drawn by Battista Ferrari in Italy in 1664 (Ragusa 2002). Three pests have been reported from North American maple trees (Acer negundo L., A. saccharinum L. and A. rubrum L.), i.e. Shevtchenkella brevisetosa, Vasates quadripedes and Rhyncaphytoptus negundivagrans. The 25 species recorded during the period 1975–1999 almost all have a North American origin (only Epitrimerus cupressi is designated as cryptogenic, because of the Mediterranean origin of its host Cupressus sempervirens L.). During the period from 2000 to 2007, one species alien to Europe, Rhyncaphytoptus bagdasariani, has been recorded as being introduced from Asia and the serious pest Aceria fuchsiae (a species on the European quarantine list) was introduced from South America. As for other phytophagous mites, the most probable explanation for the acceleration in the pace of introductions of alien eriophyids is intensification of international trade. Most of these alien species inhabit ornamental trees and shrubs, flowers and potted ornamental plants.

Some alien parasitic mites have invaded Europe with rodents such as muskrats and brown rats. The muskrat (*Ondatra zibethicus* L.) is an invasive rodent native to North America. It was introduced around 1905, by humans as a fur resource in several parts of Europe, as well as in Asia and South America. Six species of mites, native from North America (Bauer and Whitaker 1981, Whitaker 2007), have invaded Europe grasping its fur (Glavendekić et al. 2005, Šefrová and Laštůvka 2005). The first report of muskrat mites was recorded in 1955, and a second in 2000, both in Czech Republic. Two other parasitic species, *Laelaps echidninus* and *Ornithonyssus bacoti*, are also alien ectoparasites of rodents that have invaded Europe and were identified in the 1950's (Šefrová and Laštůvka 2005), but the exact pathway of introduction is not known. One possible vector is the wild brown rat, *Rattus norvegicus* (Berkenhout). Thought to have originated in northern China, this rodent spread in Europe in the middle ages and is now the dominant rat in the continent.

Birds are vectors of a second group of alien parasitic mites, that include *Epider-moptes bilobatus* and *Ornithonyssus bursa*, both identified in the 1950's, in the Czech Republic (Šefrová and Laštůvka 2005). The exact route of introduction is not known with confidence, but a possible vector is the chicken (*Gallus gallus domesticus* L.). In the 20thcentury, with the intensifications of poultry production, concerns have been raised about the increasing risk of transfer of diseases and mites (from chickens to native bird species).

Whereas the exact date of arrival of alien mites is generally unknown, deliberately released biological control agents are the exception to this rule. Among them, three phytoseiids are mainly used as predatory species against pests (McMurtry and Croft 1997). *Phytoseiulus persimilis* was introduced for the first time in the 1970's in Bulgaria and Czech Republic (EPPO 2002, Šefrová and Laštůvka 2005). *Neoseiulus californicus* was introduced for the first time in 1991 in Great Britain (EPPO 2002). It was also introduced at the same period in the Czech Republic (EPPO 2002, Šefrová and Laštůvka

2005). The third introduced mite is *Iphiseius degenerans*. It is native from the Mediterranean region and was introduced for the first time in 1993 in Czech Republic (EPPO 2002, Šefrová and Laštůvka 2005). Nowadays, these three biological agents have been introduced in most European countries.

7.4.4 Biogeographic patterns of the mite species alien to Europe

7.4.4.1 Origin of the mite species alien to Europe

Figure 7.4.3. presents the region of origin of the 101 alien species of mites. Most of the alien mite species (52%) came from North America, then from Asia (25%), and Central and South America (10%). The origin of phytophagous alien mites can usually be inferred from the origin of the host plant. These mites are dispersed over long distances mainly by the introduction of plant material and spread further by plant cultivation in newly colonized regions. Aerial distribution is possible and most frequent, but mainly over short distances (Margolies 1993, Margolies 1995). In the case of highly polyphagous species such as several Tetranychidae, their ubiquity and highly diverse host uses might be misleading and the origin can be difficult to ascertain. Twelve out of 27 alien Tetranychidae originated in North America, nine in Asia and only five in Central and South America. Temperate regions provide the majority of the alien species (16 vs. 11 for tropical areas).

The majority of eriophyoid species are mono- or oligophagous and are distributed within the host range. North America appears to be the dominant source of the alien eriophyoid fauna with half of the species originating from this continent. Around 26% of species originate from Asia, and less than 10% from South America. A few species are designated as cryptogenic or with questionable origin. For example, Rhyncaphytoptus negundivagrans, although described from Hungary, probably originated from North America with its host plant, Acer negundo. Whereas the camellia rust mite, Cosetacus cameliae (described from California) was probably introduced to Europe from the USA, it probably has an Asian origin considering that Camelia japonica L. comes from subtropical and tropical regions of Southeast Asia. The pouch gall mite of plum leaves, Eriophyes emarginatae, first discovered in the USA, has also been recorded in Serbia and Japan. This mite is very closely related to the European *E. padi* (Nalepa) (Petanović 1997) and may even be the same species, with synonymous names (Keifer 1975). Epitrimerus cupressi was described from North America, but according to the origin of its host plant Cupressus sempervirens, which is from the Mediterranean region, the mite probably has an European origin too. The gall mite *Phytoptus hedericola* (Phytoptidae) is native from South Africa (Glavendekić et al. 2005), and Trisetacus chamaecypari (Phytoptidae) from North America (Ostojá-starzewski and Halstead 2006, Smith et al. 2007).

Among the false spider mites (Tenuipalpidae), Brevipalpus californicus, B. obovatus and Tenuipalpus pacificus originated from Central and South America, and Florida

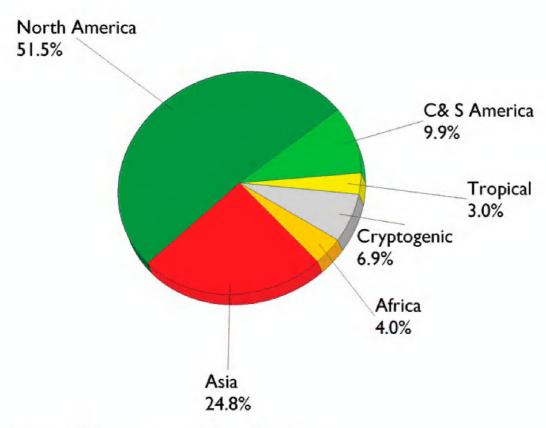


Figure 7.4.3. Origin of the mite species alien *to* Europe.

(USA) (Denmark 1968, Manson 1967). Six alien species of rodents bear parasitic mites originating from North America, and belong to the families Listophoridae (four species), Laelapidae (one species), and Myocoptidae (one species). In their native country, they are all ectoparasites of murskrats. There are also some bird parasites: one species of Epidermoptidae, *Epidermoptes bilobatus*, is an ectoparasite native from South Asia, and *Ornithonyssus bursa* is probably native from Trinidad.

A single *Varroa* species, *V. destructor*, is alien to Europe (Griffiths and Bowman 1981). Its native range is South East Asia, where it was originally confined on its original host, the Asian honeybee, *Apis cerana* F. This mite came to be a parasite of the European honeybee, *Apis mellifera*, in the mid-twentieth century. Importation of commercial *A. mellifera* colonies into areas with *A. cerana* brought the previously allopatric bee species into contact and allowed *V. destructor* to switch to the new host

7.4.4.2 Distribution in Europe of the alien mite species

Alien mite species are not evenly distributed throughout Europe. Large differences in the number of aliens are noticed between countries (Figure 7.4.4) but it may reflect differences in sampling efforts and in the number of local taxonomic specialists.

Among the Tetranychidae, 19 alien species are found around the Mediterranean Basin and 12 in the rest of Europe. With relatively warm winters, the Mediterranean region provides suitable climatic living conditions for many species of temperate climates, but also for the establishment of many species of tropical or sub-tropical origin. Except for *Panonychus citri* and the cryptic species *Tetranychus ludeni*, which can be found in glasshouses in Europe, all tropical alien spider mites are restricted to the area around the Mediterranean Sea.

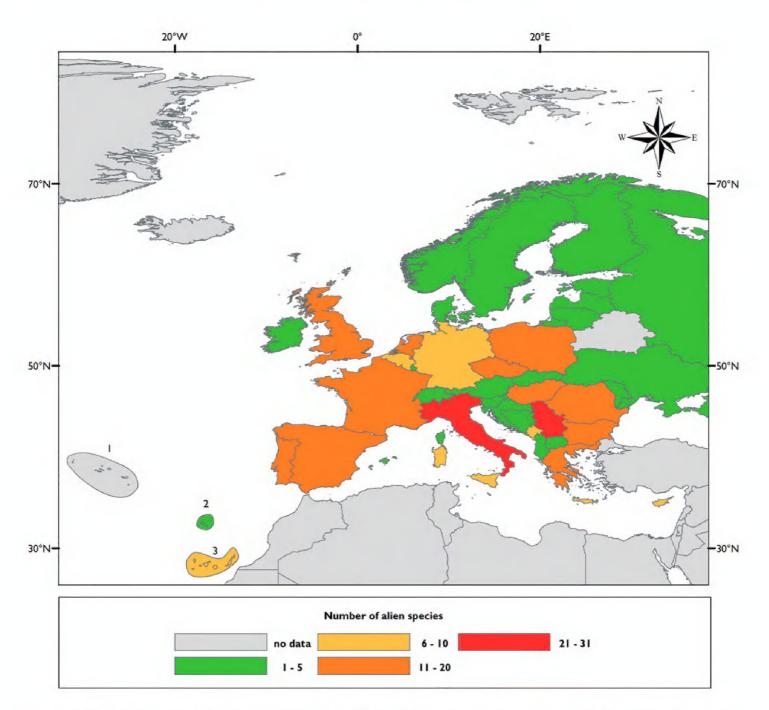


Figure 7.4.4. Comparative colonization of continental European countries and islands by mite species alien *to* Europe. Archipelago: I Azores 2 Madeira 3 Canary Islands.

Most alien Eriophyids have a very restricted distribution. More than 40% of the species have been observed in only one country (17 species), more than 40% (21 species) in 2–5 countries, and approximately 20% (7 species) in 6–11 countries. Eight European countries have no recorded occurrence of alien eriophyoids to date. Only one species, the pear blister mite *Eriophyes pyri* (which has cryptogenic status), has been recorded from 32 European countries. Besides *E. pyri*, the more widely distributed eriophyoid species are: *Aceria erinea, A. loewi, A. sheldoni, Aculops pelekassi* and *Eriophyes canestrini*. The gall mite *Phytoptus hedericola* (Phytoptidae) entered Europe in 2002 and has been observed in Serbia (Glavendekić et al. 2005). *Trisetacus chamaecypari* (Phytoptidae) entered Europe in 2002 (Ostojá-starzewski and Halstead 2006, Smith et al. 2007). The status of *Typhloctonus squamiger* (Phytoseiidae), a poorly known phytophagous mite found on trees in Italy since 1991 (Rigamonti and Lozzia 1999), is questionable.

The distribution of biological agents belonging to the Phytoseiidae family is well-known. *Phytoseiulus persimilis* is now present in nearly all of Europe (Table 7.4.1)

(EPPO 2002). *Neoseiulus californicus* has been found in the same countries except Austria, Hungary, Morocco, Slovakia, Sweden and Turkey. The third introduced phytoseid mite, *Iphesius degenerans*, is also present in several countries (Table 7.4.1).

The broad mite *Polyphagotarsonemus latus* (Tarsonemidae) is now cosmopolitan. In Europe, it was reported for the first time in 1961 and since then the mite has invaded almost all countries (Table 7.4.1) (CAB-International 1986, Fan and Petit 1998, Natarajan 1988, Parker and Gerson 1994); it is potentially now in all parts of Europe.

Three species of false spider mites (Tenuipalpidae) are major invaders in Europe. *Brevipalpus californicus*, found in 316 orchid and tree species of 67 genera and 33 families, was first recorded in 1960 and is mainly observed in citrus trees around the Mediterranean basin (Denmark 1968, Manson 1967). The privet mite, *Brevipalpus obovatus* is found in 451 herb, ornamental and shrub species (19 genera, 55 families) (Manson 1967) has been recorded from Austria, Cyprus, France, Germany, Israel, Netherlands, Serbia and Spain (Manson 1967). *Tenuipalpus pacificus* (the Phalaenopsis mite) is found in greenhouses of *Phalaenopsis* orchids in Germany, Great Britain, Netherlands and Serbia (Denmark 1968, Manson 1967).

The introduced range of *Varroa destructor* is practically worldwide. It was first reported in Eastern Europe in the mid- 1960s and it has spread rapidly all over the continent. Two different genotypes, characterized by mitochondrial DNA sequences, have spread as independent clonal populations (Solignac et al. 2005), the Korean and the Japanese haplotypes, the latter having been found, besides Asia, in the Americas only.

7.4.5. Pathways of introduction in Europe of alien mite species

Although colonisation routes are poorly documented for the Tetranychidae, it is known that many species travel with their host plant. Small organisms like tetranychids are easily transported with plant material (leaves and in bark crevices). Only five species feed mainly on herbaceous plants (*Tetranychus evansi*, *T. macfarleni*, *T. sinhai*, *Schizotetranychus parasemus*, and *Petrobia lupini*), whereas all other alien species in the family feed on perennial shrubs.

As for tetranychids, the horticultural and ornamental trade is probably the most important factor for accidental introductions of almost all species of alien Eriophyoidae. Just a few species of Eriophyoids are on European quarantine lists, as plants are rarely inspected for presence of these mites. Infested plant material is not regularly intercepted at borders even in the case of important pests such as the grape rust mite *Calepitrimerus vitis* (Nalepa) or the blackberry fruit mite *Acalitus essigi* (Hassan), which are frequently disseminated with plant seedlings. During recent decades more than 50% of aliens were imported with ornamental plants. Among eriophyids, which are obligate plant parasites, only one trophic group which is associated with weeds, can be subject to intentional introduction. Although these mites were recently nominated as potential agents for classical biological control of weeds (few species are imported for this purpose), they have not yet been used for this purpose in Europe. Four species of

alien eriophyoids which were probably introduced along with their host plants may have the potential as biological control agents of serious alien weed pests. In particular, *Aceria ambrosiae* can be used against the allergenous weed *Ambrosia artemisifolia* L. that was imported into Europe from North America.

As for other phytophagous species, the broad mite *Polyphagotarsonemus latus* (Tarsonemidae) has mainly been dispersed by human activities, but also by wind or insect transfer. Movement by insects should not be neglected: this concerns almost only females that get attached to the legs of aphids and the whiteflies *Bemisia argentifolii* (Bellows and Perring), *Bemisia tabaci* (Gennadius) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae) (Fan and Petit 1998, Natarajan 1988, Parker and Gerson 1994).

Although including important crop pest species, the dispersal potential of false spider mites (*Brevipalpus* spp.), Tenuipalpidae, remains unclear (Childers et al. 2003a, 2003b).

Intentional introductions of mites represent a low proportion of alien arrivals. Only three phytoseeid predators were introduced purposely for biological control and have established. Some of these biological control agents were released in the field but others were first released in glasshouses, and then escaped and became established outdoors.

International travel and commerce has facilitated the dispersal of *Varroa destructor*. Once established in a new region, the mite spreads using drifting, robbing, and swarming behaviour of the host. Human mediated varroa dispersion also occurs via apicultural practices.

7.4.6. Ecosystems and habitats invaded in Europe by alien mite species

Alien mites established in Europe predominantly live in agrosystems or anthropogenic environments (ca. 92%; Figure 7.4.5). This is especially verified in Tetranychidae and Eriophyidae. Among eriophyoids, some are present in man-made habitats, parks and gardens (22 species), agricultural lands (13 species), and greenhouses (10 species); very few species inhabit woodland and forest, costal, alpine or sub alpine habitats. Most alien species in this superfamily are leaf vagrants (13 species). Twelve species cause leaf galls, erinea* and leaf rolling, 11 cause leaf and/or fruit russeting or other type of discolouration, six live predominantly in buds causing bud galls, three species cause stunting of whole plants and/or plant organs and two cause flower and/or fruit deformations. Among the leaf gall makers, the most important horticultural pests are distributed in many European countries, such as E. pyri, A. erinea, A. tristriata or, such as A. fuchsiae which is on quarantine lists. Among the rust mites, only a few are important horticultural pests like A. theae, A. pelekassi and C. carinatus. Most species are pests of ornamental trees, shrubs or flowering plants, having an important aesthetic impact on plants in parks and streets in most European towns and cities (i.e. A. gleditsiae, A. ligustri, A. petanovicae, S. strobicus, P. chrysanthemi), an exception being A. sawatch-

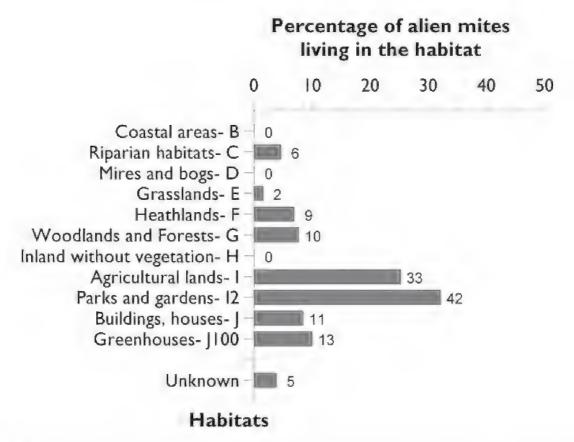


Figure 7.4.5. Main European habitats colonized by the established alien species of mites. The number over each bar indicates the absolute number of alien dipterans recorded per habitat. Note that a species may have colonized several habitats.

ensae which inhabits weeds. Two Eriophyoids which cause plant stunting, *A. paradianthi* and *T. califraxini*, are important pests of ornamental plants and one species, *A. ambrosiae*, is a potential biocontrol agent against the alien weed *Ambrosia artemisifolia*. Two species which cause flower and/or fruit deformations, *A. alpestris* and *A. sheldoni*, are respectively pests of *Rhododendron* and citrus trees.

The gall mite *Phytoptus hedericola* lives on ivy (*Hedera helix* L.) and *Trisetacus laricis* switched from American larch to European larch (*Larix decidua* Mill.).

The broad mite *Polyphagotarsonemus latus* (Tarsonemidae) has a very short life cycle of a few days, damaging crops abruptly. Being highly polyphagous, the species has been reported on 57 plant families (Gerson 1992) both in open field crops and in greenhouses. This is an important pest of crops and ornamental plants such as azaleas, castor bean, chillies, citrus fruits, cotton, cucumber, mango, papaya, pepper, potato, sweet potato, tea, tomato and winged bean (Gerson 1992, Glavendekić et al. 2005, Heungens 1986, Raemaekers 2001). Nevertheless, in Europe this mite is found mainly in greenhouses because the mite cannot survive winter conditions outdoors.

False spider mites (*Brevipalpus* spp.; Tenuipalpidae) present a risk of invasion in greenhouses. *Brevipalpus obovatus* (the privet mite) is found on ornamentals and shrubs like citrus and azaleas and could become of great importance in glasshouses for ornamentals (Childers et al. 2003a, 2003b). *Tenuipalpus pacificus* (the Phalaenopsis mite) is one of the rare monophagous mites in the family, but it is a very destructive pest of orchids under greenhouses, mainly because it has several generations per year and has a two-month life cycle (Denmark 1968, Manson 1967).

A Pyroglyphidae mite, *Dermatophagoides evansi*, is a cosmopolitan free-living species, often encountered in synanthropic situations and has probably been accidentally introduced by humans (Bigliocchi and Maroli 1995, Hughes 1976).

7.4.7. Ecological and economic impact of alien mite species

Seven species of alien Tetranychidae are important pests. On citrus, four alien species are found: *Panonychus citri*, *Eotetranychus lewisi* (also on grapes) *Eutetranychus banksi* and *E. orientalis*, the last presently spreading to Southern Portugal and Spain from Huelva to Murcia and Alicante. *Oligonychus perseae* is found on avocado and produces very severe damage in southern Spain (Malaga, Granada and Huelva) and in the Canary Islands. *Stigmaeopsis celarius* is found on bamboos and causes important visual damage to these ornamental plants. *Tetranychus evansi* is found on solanaceous crops and can reach very high density as observed in France, Spain and Canary Islands. All these mites are present in the Mediterranean Basin, which appears to be the region most threatened by alien species. Only two of these species can be found outside the Mediterranean area: *Panonychus citri*, especially in glass-houses, and *Stigmaeopsis celarius*.

In humid citrus-growing regions of the world, eriophyoid mites are considered to be the major mite pests (Jeppson et al. 1975, McCoy 1996). Two alien species, Aceria sheldoni and Aculops pelekassi, distributed worldwide, are among the most important pests infesting citrus. The pear blister mite, *Eriophyes pyri*, widely distributed in Europe, probably does little harm to the tree, but in severe infestations, the tree leaves may become disfigured, and most importantly the mite may damage fruits (Easterbrook et al. 2008). Besides fruit orchards, species in the superfamily inhabiting wild trees in natural forests are: Aceria tristriata and A. erinea which appear to be the most common and most injurious eriophyoids found on Juglans regia L. (Castagnoli and Oldfield 1996). Among the five species of eriophyoid mites reported from commercially important beverage crops in different parts of the world, wherever tea is grown, the purple tea mite Calacarus carinatus and the pink tea mite Acaphylla theae are economically important in Southeast Asian countries, and in India (Channabasavanna 1996). Both species are aliens to Europe, reported from mainland Italy (A. theae) and from Hungary, Poland and Spain (C. carinatus). Records concerning host plant range in the case of *C. carinatus* are, besides tea, *Viburnum opulus* L. and Capsicum annuum L. (Amrine and Stasny 1994). Bearing in mind that congeneric Calacarus citrifolii has an extremely wide host range (Oldfield 1996), this might be also the case for *C. carinatus*, which would convey on the latter serious pest status in Europe. Economic impact of alien pest species of eriophyoids on ornamentals has been observed for Aculops gleditsiae on honey locust, Aceria petanovicie on lilac, Aculops ligustri on privet hedges, Aculops allotrichus on black locust, Reckella celtis on Celtis australis L., Shevtchenkella brevisetosa on Acer negundo, Vasates quadripes on silver maple, Phytoptus hederae on English ivy, and Setoptus strobicus on Pinus strobus L. (Petanović 2004). Flower and foliage aesthetic impact has been observed indoors (business centers, restaurants, shopping centers, hotels, etc.) for a few alien eriophyoids, Cecidophyopsis hendersoni causing a powdery



Figure 7.4.6. Alien mites and their damage. a Curling and rusting of black locust leaves caused by Aculops allotrichus b Chlorotic and misshapen leaves of Acer negundo caused by Shevtchenkella brevisetosa (left) and uninfested leaves (right) c Leaf rusting of lilac leaves caused by Aceria petanovicae d Aceria petanovicae, dorsal view-SEM photograph e Rusting of Pinus strobus needles caused by Setoptus strobacus f Setoptus strobacus eggs, juveniles and adults between needles of Pinus strobus g Leaf distortion and unopened damaged flower buds of chrysanthemum caused by Paraphytoptus chrysanthemi h Deformed flower heads of chrysanthemum caused by Paraphytoptus chrysanthemi i Colony of Cecidophyopsis hendersoni on Yucca leaf j Panonychus citri. (a—i Credit: Radmila Petanović; j Credit: Alain Migeon).

appearance on *Yucca* leaves, *Cosetacus cameliae* causing bud rust and abortion on flower buds of *Camelia* plants, and *Paraphytoptus chrysanthemi* causing deformed buds, hairy leaves and rust on *Chrysanthemum* (Petanović 2004).

The broad mite *Polyphagotarsonemus latus* (Tarsonemidae) and the false spider mites (*Brevipalpus* spp.) (Tenuipalpidae) are major pests of great agronomical impor-

tance because of their broad host range, worldwide distribution and economic impact (CAB-International 1986, Fan and Petit 1998, Gerson 1992, Heungens 1986, Natarajan 1988, Parker and Gerson 1994, Raemaekers 2001). The most important threat for *Brevipalpus* spp. is the spread of citrus viruses (Childers et al. 2003b).

Among parasitic mites, the hair mites (muskrat mites) are currently considered non-pathogenic for humans although they are sometimes found in the fur of other mammals. Laelaps echidninus (Laelapidae) is a common worldwide ectoparasite of the spiny rats (hystricognath rodents), wild brown rat and is occasionally found on the house mouse, cotton rat and other rodents. It is a bloodsucking mite and the natural vector of Hepatozoon muris Balf. (Protozoa, Adeleidae), a haemogregarine parasite pathogenic for white rats (Smith et al. 2007) but which should not be overlooked as a possible vector of disease to humans (Wharton and Hansell 1957). Ornithonyssus bacoti (Macronyssidae) is a parasite of rats and inhabits the area in and around the rat's nesting area. This mite is the only one of the common rat mites which frequently deserts domestic rats to bite man or his domestic and laboratory animals (Cole et al. 2005). It is also a bloodsucking mite and its bite is painful and causes skin irritation, itching and skin dermatitis in humans (James 2005). Ornithonyssus bacoti, is a known vector of the murine filarial nematode Litomosoides carinii Travasaos. In addition, it is susceptible to the transmission of endemic typhus, Rickettsia typhi (Wolbach and Todd) 1943 (= R. mooseri Monteiro) to humans (Berggren 2005, Bowman et al. 2003).

Epidermoptes bilobatus (Epidermoptidae) is a bird parasite causing avian scabies. This endoparasite burrows into the skin causing inflammation and itchiness. The skin thickens with brownish-yellow scabs, which may become secondarily infected with a fungus. It is difficult to control and can cause death. Culling infested birds is usually required (Department of the Environment and Heritage 2006). Ornithonyssus bursa (Macronyssidae) is an haematophagous natural parasite of common birds including pigeons, starlings, sparrows, Indian mynahs, poultry, robin (Berggren 2005). These pest mites and parasites are and will remain a long term problem for poultry housing (Gjelstrup and Møller 1985). Although none of these two species of mites are truly parasitic on humans and pets, they readily bite humans and are liable to cause allergies and dermatitis in human (Denmark and Cromroy 2008, James 2005). Dermatophagoides evansi (Pyroglyphidae), and a species alien in Europe, Glycyphagus domesticus (Glycyphagidae), have been accidentally introduced by humans and often encountered in synanthropic situations (Bigliocchi and Maroli 1995, Hughes 1976, Thind and Clarke 2001). Glycyphagus domesticus also occurs in bird, bat and mammal nests. It is associated with moist and humid conditions that promote the growth of mould on which they feed (Thind and Clarke 2001). Dermatophagoides evansi (Pyroglyphidae) feeds on detritus and is also found in house dust, birds' nests and poultry houses (Piotrowski 1990, Razowski 1997). Dermatophagoides evansi represents a source of airborne allergens in indoor house dust (Eriksson 1990, Musken et al. 2000) that may cause sensitization, dermatitis, rhinopharyngitis and asthma especially among farmers.

The honeybee ectoparasite *Varroa destructor* causes serious losses through feeding injury in apiaries in Europe but also almost worldwide. While the populations of the



Figure 7.4.7. Ixodidae ticks on tortoises and snakes. **a** Hyalomma aegyptium on tortoise **b** Amblyomma exornatum semi-engorged on Python head **c** Amblyomma sp. on snake head (Credits: Nicasio Brotons) **d** Female of *Varroa destructor* on abdomen of *Apis mellifera* (Credit: Alain Migeon).

parasite reach only a small size within colonies of *A. cerana* and do not damage the colony, infested *A. mellifera* colonies die. The problems with varroa control are typical of those encountered in curbing arthropod pest population. Varroas are becoming resistant to the acaricides used by beekeepers to control them. The recent discovery in several parts of the world (notably the United States of America (Harbo and Harris 2005) and Europe (Le Conte et al. 2007)) of honeybee bee colonies able to tolerate heavy infestations of *V. destructor* opens the door to lasting solutions for controlling the parasite.

A positive impact is recognized for the three mite species deliberately introduced to Europe for biological control of house flies and tetranychid mites. *Phytoseiulus persimilis* and *N. californicus* are two well-known biological control agents used against spiders mites such as *Tetranychus urticae* Koch (Garcia Mari and Gonzalez-Zamora 1999, Helle and Sabelis 1985) and *Phytonemus pallidus* (Banks) (James 2005). The third introduced mite, *Iphiseius degenerans*, targets numerous species of thrips (van Houten and van Stratum 1993, van Houten and van Stratum 1995), e.g. *Thrips tabaci* Lindeman and *Frankliniella occidentalis* (Pergande) (Albajes et al. 1999, Bartlett 1992, McMurtry and Croft 1997, Sengonca et al. 2004).

7.4.8. Alien tick species: case studies

It is difficult to ascertain if a tick may have permanent populations outside of its native range or, to the contrary, they are just isolated records. In some cases, a few examples

of a given species have been reported for a small area or found over non-resident hosts. This may result from the introduction of a few specimens, commonly immature stages. The most important means of introduction and expansion of ticks (provided that suitable climate and host is available) is by means of engorged females, because of their huge potential to lay thousands of eggs.

The movements of domestic ungulates have introduced some tick species, that may be considered to produce permanent and viable populations out of their native range. An example is the introduction of *Hyalomma dromedarii* into the Canary Islands, by the importation of dromedaries (Camelus bactrianus L.). The native range of this tick is northern Africa where C. bactrianus is the main adult host, and H. dromedarii is abundant in wide areas of Mauritania and Morocco. The current population of dromedaries in the Canary Islands was introduced from Morocco at the end of 18th Century, and it seems that this tick came into these islands using dromedary hosts. *H. dromedarii* may use a wide range of hosts in immature stages, thus increasing risk of spread and permanent establishment (Apanaskevich and Horak 2008, Apanaskevich et al. 2008). It is difficult, however, to assess the reliability of records of Hyalomma anatolicum excavatum. A recent review of the original two subspecies (*H. a. anatolicum* and *H. a. excavatum*), concluded that they should be considered as separate species, although the matter is hard to decide as both taxa have a well defined allopatric range (Apanaskevich 2003). H. excavatum is restricted to central and eastern Asia and H. anatolicum colonizes wide areas of northern Africa. The records of H. excavatum from Bulgaria, Albania, Greece, and Italy should be cautiously treated, as they may probably represent H. anatolicum imported from northern Africa with domestic ungulates, as is the case for Hyalomma detritum. The formerly recognized species H. detritum, restricted to northern Africa, is now considered to be a synonym of the European H. scupense, which occurs not only in scattered localities of mainland Europe but is present in wide areas of northern Africa. Similarly, caution should be also applied for the single record of *Hyalomma truncatum* in the Canary islands. This tick is currently known to be restricted to parts of Asia, while a close species, *H. rufipes*, is common in sub-saharan Africa. While the adults of H. rufipes feed on a variety of hosts, including domestic ungulates, the immature stages commonly attach to diverse passerine birds. Most of these birds perform long distance travel in their migratory flights from Africa to Europe, and they have been found carrying hundreds of immature ticks (Hoogstraal 1956). However, as mentioned above, it is difficult for a population of nymphs to produce a viable and permanent population of resident ticks. To our knowledge, H. rufipes has been recorded only in Cyprus and Macedonia (Apanaskevich and Horak 2008), and we still do not know if these are permanent populations or only accidental records on their passerine hosts on migration to lower latitudes from sub-saharan Africa.

The scenario for the tortoise tick, *Hyalomma aegyptium*, is however different. Its presence outside northern Africa has been reported in countries such as Romania, Spain, Italy, Greece, Bulgaria, Croatia, and even farther north in Belgium (Siroky Pet al. 2007). The tick has permanent populations in areas of southern Russia (Robbins et al. 1998). There have been also introductions of this tick by tortoises imported form

northern Africa or eastern Europe, where this tick is common. The only record of a permanent population of *H. aegyptium* as a consequence of an accidental importation recorded for eastern Spain (Brotóns and Estrada-Peña 2004). Since the ticks attach to portions of the neck and legs of the host body, it may be difficult to find feeding stages even after careful observation of the hosts. In the reported case of introduction of several specimens of *Testudo graeca* infested by ticks, the hosts were kept in a large private garden with a Mediterranean-type climate and vegetation. After some years of recurrent tick parasitism in the tortoises without new importations and repeated treatments, it was realized that the tick had permanent populations in the garden, and the hosts became infested according to the seasonal activity of the ticks.

An interesting case of tick introduction into mainland Europa are ticks commonly found on snakes, like *Amblyomma latum* and *A. exornatum* (both formerly in the genus *Aponomma*). These ticks feed for a long period on the host, and owing to their small size and preference to feed under host scales, they are commonly unrecognized while importing a host out of its native range. *Amblyomma latum* is a very common parasite of *Python spp.*, which is becoming increasingly popular as a pet in Europe. The only known case of an importation of *A. exornatum* was noticed on specimens of *Varanus niloticus* that arrived into Spain (Estrada-Peña (Unpubl.)). These imported ticks founded a permanent population in the terrarium where the lizards live, under suitable conditions of high relative humidity and controlled temperature.

A very peculiar case of tick introduction is an alien *in* Europe, the brown dog tick, *Rhipicephalus sanguineus*. While feeding on domestic dogs, this tick is endophilic and is normally restricted to the Mediterranean region, being abundant in kennels, human constructions and private gardens where dogs remain unprotected against tick bites. Because of its endophilic behaviour, this tick may survive independently of prevailing environmental conditions, since human habitations buffer harsh climate. Therefore, unprotected pets travelling may harbor feeding ticks, and introduce them to uninfested areas which might be far from their native range. Such cases of introduction have been commonly recorded in the United Kingdom and northern European countries (Garben et al. 1980, Sibomana et al. 1986), as well as in Czech Republic (Černý 1985). Although there are as yet no reports of its establishment outdoors, this tick could become established out of its former native range as a consequence of global warming.

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Table 7.4.1. List and characteristics of the mite species alien to Europe. Status: A: Alien to Europe; C: cryptogenic species. Country codes abbreviations refer to EUNIS (see Appendix II).

P	Native range	1st record	Invaded	Habitat	Hosts	References
A D A A A A		in Europe	countries			
A A A A A						
O	s Asia South West	2002, RS	RS	12, X11	Ulmus, Quercus macranthera, Salix caprea	Petanović (2004)
A A	s North America?	1960, HU	HU, RS	12, X11	Acer negundo	Petanović (in prep.), Ripka (2007)
A A						
A A A A	Asia- Tropical	1948, CZ	CZ	I, J	Gallus	Šefrová and Laštůvka (2005)
A A A A						
A A A A	s Asia	1983, IT	IT, ES	12	Camellia	Fauna Europaea (2009), Pérez Otero et al. (2003)
A A A	s North America	1997, RS	RS	12, X11	Hedera helix	Petanović and Stanković (1999)
A A	s North America	1999, RS	RS	J(J1–J4)	Ambrosia psilostachya, Ambrosia artemisifolia	Petanović (1999)
Y .	s North America	1981, RS	RS	X24, X25	Cucumis sativus	Petanović (1988), Petanović (1997)
<	s Asia South West	1998, RS	RS	12, X11	Berberis californica, Mahonia dyctiota	Petanović (1998)
Acerta ermea (Ivalepa, A Prytopnagous 1891)	s Asia South West	1903, BG	BE, BG, CZ, GB, LU, ME, RO, RS	I1, I2, X11, X13	Juglans regia	Petanović (1988)

Family	Status	Regime	Native range	1st record	Invaded	Habitat	Hosts	References
Species				in Europe	countries			
Aceria ligustri	A	Phytophagous	North	1995, RS	BE, HU, PL,	12,FB, X11	Ligustrum	Petanović (1997), Petanović
(Keifer, 1943)			America		RS		ovalifolium,	(1998), Soika and Labanowski
							Ligustrum sp.	(1998), Witters et al. (2003)
Aceria neocynarae	A	Phytophagous	North	1998, ES	GR, IT-SIC,	Ι	Cynara	Fauna Europaea (2009),
(Keifer, 1939)			America		PT, ES		scolimus	González Núñez et al. (2002)
Aceria paradianthi	A	Phytophagous	North	1987, GR	1987, GR IT, PL, GR	J100	Dianthus sp.	Anagnou-Veroniki et al.
(Keifer, 1952)			America					(2008), Fauna Europaea (2009)
Aceria petanovicae	A	Phytophagous	Medi-	1939, IT	FI, GB, HU,	12, X11	Syringa	Fauna Europaea (2009), Fauna
Nalepa, 1925			terranean East		IT, RS			Italia, Petanović and Stanković (1999), Ripka (2007)
Aceria sawatchense	A	Phytophagous	North	1981, RS	RS	J (J1-J4)	Polygonum	Petanović et al. (1983)
Keifer, 1965			America				douglasii ssp.	
							johnstoni,	
							Polygonum	
, H 1 1	<	1-		17th 17T	דנו ער סמ	I V13	Iapauloiluiii	, , , , , , , , , , , , , , , , , , ,
Aceria spelaoni (Ewing,	V	Fnytopnagous	Asia :	1/",11	ES, GR, 11,	CIV,	Citrus	Wiljuskovic and lomasevic
1937)					IT-SAR, IT- SIC, ME, PT			(1975)
Aceria tristriata	A	Phytophagous	Asia South	1903, RS	BG, CZ, GB,	X13	Juglans	Petanović (1996), Trotter
(Nalepa, 1890)			West		LU, ME, RS			(1903)
Aculops allotrichus	A	Phytophagous	North	1912, RO	BG, CZ, RO			
(Nalepa, 1894)			America	-				
Aculops fuchsiae	А	Phytophagous	South	2003, FR	DE, FR, GB	11,12	Fuschia	Deutsche Dahlien, Fuchsien,
Keifer, 1972			America					Gladiolen und Kübelpflanzen, Ostojá-Strazewski (2007)
Aculops gleditsiae	A	Phytophagous	North	1993 RS	HU, IT, RS	X11	Gleditsia	Fauna Italia, Petanović (1993),
(Keifer, 1959).			America				triacanthos	Petanović (1997), Ripka
								(2007), Ripka and De Lillo
								(1997)

Family	Status	Regime	Native range	1st record	Invaded	Habitat	Hosts	References
Species Aculops pelekassi (Keifer, 1959)	A	Phytophagous	Asia	in Europe 1958, GR	ES, GR, IT, IT-SAR,	I, X13	Citrus	Mijušković and Tomašević (1975)
					MT			
Aculops rhodensis (Keifer, 1957)	A	Phytophagous	North America	1997, HU	HU, IT	X11, X13	Salix alba, Salix elegnos	Fauna Italia
Aculus ligustri Keifer,	A	Phytophagous	North	1993, IT	HU, IT, RS	X11, X13	Ligustrum	Fauna Italia, Petanović and
1938			America				ovalifolium , Ligustrum sp.	Stanković (1999), Ripka (2007)
Anthocoptes punctidorsa Keifer, 1943	A	Phytophagous	North America	1991, IT	II	12, FB	Ulmus laevis, U. pumila	Rigamonti and Lozzia (1999)
Anthocoptes transitionalis	A	Phytophagous	North	1989, RS	RS	X13	Acer rubrum,	Glavendekić et al. (2005),
Hodgkiss,1913			America				A. monspessu- lanum	Petanović (1997)
Calacarus carinatus	A	Phytophagous	Asia	1983, IT	ES, HU, IT,	12	Camellia,	Fauna Europaea (2009)
(Green, 1890)					PL		Capsicum, Viburnum	
Cecidophyes malifoliae	A	Phytophagous	North	1991, RS	RS	X13	Malus x	Petanović and Stanković
Parrot, 1906			America				domestica,	(1999)
							Aremonia agrimonoides	
Cecidophyopsis	A	Phytophagous	North	1991, RS	RS, PL	J100, J1	Yucca glauca,	Glavendekić et al. (2005),
hendersoni (Keifer,1954)			America				Yucca gloriosa	Labanowski (1999), Petanović (2004)
Coptophylla lamimani	A	Phytophagous	North	1981, RS	IT, RS, ME	12, FB, X13	Corylus	Petanović (1988), Rigamonti
(Keifer, 1939)			America				avellana, Corylus colurna	and Lozzia (1999)
Cosetacus camelliae	A	Phytophagous	North	1990, ME	ES, ME	12, J100	Camelia	Estación Fitopatolóxica do
Keifer, 1945			America				japonica	Areeiro (1998), Petanović
								(1997), Petanović and Stanković (1999)

Family	Status	Regime	Native range	1st record	Invaded	Habitat	Hosts	References
Species				in Europe	countries			
Epitrimerus cupressi Keifer, 1939	O	Phytophagous	California?		FR, ME	12	Cupressus sempervirens	Guttierez et al. (1986), Petanović (1993)
Eriophyes emarginatae Keifer,1939	A	Phytophagous	North America	1978, RS	RS	I, X13,G1	Prunus emarginata, P. americana, P.domestica	Petanović (1997), Petanović and Dobrivojević (1987)
Eriophyes pyri (Pagenstecher, 1857)	O	Phytophagous	Cryptogenic	1903, ME	AT, BA, BE, BG, CH, CY, CZ, DE, DK, ES, FI, FR, GB, GR, GR-CRE, HR, HU, IE, IT, IV, MD, MK, MT, NL, NO, PL, PT, RO, RU, SE, SI, YU		Pear, apple, plum	Bebić (1955), Fauna Europaea (2009), Hadžistević (1955), Trotter (1903)
Paraphytoptus chrysanthemi Keifer,1940	A	Phytophagous	North America	1997, RS	RS	X25,J100	Chrysan- themum morifolium	Petanović (1997), Petanović and Stanković (1999)
Phyllocoptes amaranthi (Corti, 1917)	A	Phytophagous	South America	1981, RS	RS	J (J1–J4)	Amaranthus muricatus, A. retroflexus	Petanović et al. (1983)
Phyllocoptes azaleae Nalepa, 1904	A	Phytophagous	Asia- East	1952, CZ	BG, CZ, DE, IT, NL	5	Rhododendron	Fauna Europaea (2009), Šefrová and Laštůvka (2005)
Reckella celtis Bagdasarian,1975	A	Phytophagous	Armenia	1995, RS	MK, RS	G1, X13	Celtis caucasiaca, Celtis australis	Petanović et al. (1997)

Species Shevtchenkella branicatood		Megille	Matter Lange	nional ist	Illvaucu	Habitat	110313	Meleficies
Shevtchenkella				in Europe	countries			
bronicotoca	A]	Phytophagous	North	1999, RS	HU, PL, RS	X11, X24	Acer	Petanović (in prep.)
01601361034			America				negundo. A.	
(Hodgkiss, 1913)							negundo var.	
							californicum,	
							A.campestre	
Shevtchenkella	A	Phytophagous	North	1989, RS	RS	J (J1–J4)	Erigeron	Petanović and Stanković
erigerivagrans (Davis,			America				strigosus,	(1999)
1964)							Taraxacum	
							officinale,	
							Artemisia	
Tegolophus califraxini	A	Phytophagous	North	1988, IT	HU, IT	I2, X10–X13,	Fraxinus	Fauna Italia, Ripka (2007),
(Keifer, 1938)			America			X20	angustifolia	Ripka and De Lillo (1997)
Vasates quadripedes	A	Phytophagous	North	1957, LV	1957, LV HU, LV, RS,	12,FB	Acer	Petanović and Stanković
Shimer 1869			America		PL		saccharinum,	(1999), Ripka (2007),
							A.pseudo-	Shetchenko and Rupais
							platanus, A.	(1964), Soika and Labanowski
							rubrum	(1999)
Ixodidae								
Amblyomma latum Koch 1868	A	parasitic/predator	Africa	2004, ES	ES	ជ	Reptile,	Brotóns and Estrada-Peña
Ambhomma exornatum	A	Parasitic/predator	Africa	2004. F.S	R.S.	ŢŢ	Rentile.	Estrada-Peña (Unnuhl.)
Koch, 1844						1	phyton	(**) J
Dermacentor variabilis	A	parasitic/predator	North	?, DK	DK	Ŋ	Dog (transmit	
(Say, 1821)			America				Lyme disease)	
Hyalomma aegyptium	A	parasitic/predator	Africa	1911, DE	AL, BE, BG,	Ι	Tortoises	Brotóns and Estrada-Peña
(L., 1758)					CY, DE, ES,		(transmit	(2004), Feider (1965),
					FR, GB, GR,		Borellia)	Neumann (1911), Robbins
					GR-CRE, IT,			et al. (1998), Schulze (1927),
					PT, RO, RU			Siroky Pet al. (2007)

Family	Status	Regime	Native range	1st record	Invaded	Habitat	Hosts	References
Species				in Europe	countries			
<i>Hyalomma anatolicum</i> Koch 1844	A	parasitic/predator	Cryptogenic	1929, CY	CY	F4, F5, F6, F7	Cattle	Apanaskevich (2003), Schulze and Schlottke (1929)
Hyalomma dromedarii Koch 1844	A	parasitic/predator	Africa	1929	BG, ES-CAN	F4, F5, F6, F7	Camels	Drenski (1955), Schulze and Schlottke (1929)
Hyalomma excavatum Pomerantsev 1946	A	parasitic/predator	Cryptogenic	1940	AL, BG, CY, ES-CAN, GR, GR- CRE, IT	F4, F5, F6, F7	Cattle	Apanaskevich (2003), Battelli et al. (1977), Drenski (1955), Rosicky et al. (1960)
Hyalomma truncatum Koch 1844	A	parasitic/predator	Cryptogenic	1956 ES- CAN	ES-CAN	F4, F5, F6, F7 Cattle	Cattle	Hoogstraal (1956)
Rhipicephalus rossicus Yakimov & Kolyakimova, 1911	A	parasitic/predator	Cryptogenic	1965, RO RO	RO	F4, F5, F6, F7	Domestic animals, hedgehogs, occasionally humans (transmit Crimean congo haemorragic fever)	Feider (1965)
Laelapidae								
Laelaps echidninus Berlese, 1887	A	parasitic/predator	Asia- Tropical	1955, CZ	CZ	Ð	spiny rat	Šefrová and Laštůvka (2005), Smith et al. (2007), Wharton and Hansell (1957)
Ondatralaelaps multispinosus (Banks, 1909)	A	parasitic/predator	North America	1955, CZ	CZ	С	Muskrat	Šefrová and Laštůvka (2005)
Listrophoridae								
<i>Listrophorus americanus</i> Radford, 1944	А	parasitic/predator	North America	1955, CZ	CZ	C, I	muskrat	Bauer and Whitaker (1981), Šefrová and Laštůvka (2005), Whitaker (2007)

Family	Status	Regime	Native range	1st record	Invaded	Habitat	Hosts	References
Listrophorus dozieri Redford, 1994	A	parasitic/predator	North America		CZ	C, I	muskrat	Bauer and Whitaker (1981), Šefrová and Laštůvka (2005), Whitaker (2007)
Listrophorus faini Dubinina, 1972	A	parasitic/predator	North America	2004, CZ C	CZ	C, I	muskrat	Bauer and Whitaker (1981), Šefrová and Laštůvka (2005), Whitaker (2007)
Listrophorus validus Banks, 1910	А	parasitic/predator	North America	2004, CZ	CZ	C, I	muskrat	Bauer and Whitaker (1981), Šefrová and Laštůvka (2005), Whitaker (2007)
Macronyssidae								
Ornithonyssus bacoti (Hirst, 1913)	А	parasitic/predator	Asia- Tropical	1952, CZ C	CZ	G, I, J	tropical rat, rat, mices, little rodents	Bowman et al. (2003), Cole et al. (2005), Easterbrook et al. (2008), James (2005), Šefrová and Laštůvka (2005), Whitaker (2007)
Ornithonyssus bursa (Berlese)	A	parasitic/predator	C & S America	1948, CZ C	CZ, DK	G, I, J	birds, mammals	Berggren (2005), Denmark and Cromroy (2008), Gjelstrup and Møller (1985), James (2005)
Myocopidae								
Myocoptes ondatrae Lukoschus & Rouwet, 1968	A	parasitic/predator	North America	2004, CZ C	CZ	C, 1	Muskrat	Bauer and Whitaker (1981), Šefrová and Laštůvka (2005), Whitaker (2007)
Phytoptidae								
Phytoptus hedericola Keifer, 1943	A	Phytophagous	South Africa	2002, RS R	RS	12, X11	Hedera helix	Glavendekić et al. (2005)
Setoptus strobicus Keifer, 1966	A	S	North America	2005, RS R	RS	G3E, X25, X11 Pinus strobus	Pinus strobus	Petanović (in prep.)
Sierraphytoptus alnivagrans Keifer, 1939	А	Phytophagous	North America	2007, RS R	RS	, Geo. G1	Alnus glutinosa	Alnus glutinosa Petanović (in prep.)

Family	Status	Regime	Native range	1st record	Invaded	Habitat	Hosts	References
Species				in Europe	countries			
Trisetacus chamaecypari Smith, 1977	A	Phytophagous	North America	2002	GB	12	Chamecyparis, lawsonianna, C. nootkaensis, Cupressus macrocarpa, Juniperus	Ostojá-starzewski and Halstead (2006), Smith et al. (2007)
Phytoseiidae			_				C -	
Phytoseiulus persimilis Athias-Henriot 1957	A	parasitic/predator	South America	1974,CZ	BG, CZ, BE, DE, ES, GB, IT		Predator of Tetranychus	Bartlett (1992), Croft et al. (1998), Easterbrook (1996), EPPO (2002), Garcia Mari and Gonzalez-Zamora (1999), Helle and Sabelis (1985), McMurtry and Croft (1997), Šefrová and Laštůvka (2005)
Amblyseius (Neoseiulus) californicus (McGregor 1954)	A	parasitic/predator	North America	1991, GB	BG, CZ, GB, IT		Predator of Tetranychus	Croft et al. (1998), Easterbrook (1996), EPPO (2002), Garcia Mari and Gonzalez-Zamora (1999), Helle and Sabelis (1985), McMurtry and Croft (1997), Šefrová and Laštůvka (2005)
Typhloctonus squamiger Wainstein 1960 Pyrodynhidae	A	Phytophagous	Cryptogenic	1991, IT	IT		Acer platanoides, Prunus serratulata	Rigamonti and Lozzia (1999)
Dermatophagoides evansi Fain, Hughes et Johnston, 1967	A	parasitic/predator	North America	Unknown	NL, NO, PL, IT		house dust	Bigliocchi and Maroli (1995), Eriksson (1990), Hughes (1976), Musken et al. (2000), Piotrowski (1990), Razowski (1997), Thind and Clarke (2001)

Family	Status	Regime	Native range	1st record	Invaded	Habitat	Hosts	References
Species				in Europe	countries			
Tarsonemidae								
Polyphagotarsonemus latus (Banks, 1904	A	Phytophagous	Sri Lanka	IT, 1965	DK, ES, GB, IT, IT-SAR, IT-SIC, NL, RO, RS, BE, DE	Н	polyphagous: crops, vegetables, fruits and leaves	CAB-International (1986), Fan and Petit (1998), Gerson (1992), Heungens (1986), Natarajan (1988), Parker and Gerson (1994), Raemaekers (2001)
Tenuipalpidae								
Brevipalpus californicus (Banks, 1904)	A	Phytophagous	North America	IT, 1998	CY, FR, GR- CRE, GR, IT, IT-SAR, IT- SIC, PT, IL	12, J100	Citrus, Camellia sinensis	CAB-International (1986), Childers et al. (2003a), Childers et al. (2003b)
Brevipalpus lewisi (McGregor 1949)	A	Phytophagous	North America	Unknown	BG, FR, GR, RO	12, J100	Citrus, ornamentals	Childers et al. (2003a)
Brevipalpus phoenicis (Geijskes 1939)	A	Phytophagous	Tropical	IT, 1998	ES, GR, IT, NL	12, J100	Polyphagous, Citrus, Gardenia, Hibiscus, Ilex, Ligustrum; Ficus, Phoenix,	Childers et al. (2003a), Childers et al. (2003b)
Brevipalpus obovatus Donnadieu, 1875	A	Phytophagous	North America	IT, 1986	AT, FR, DE, IL, NL, SP, RS, BE, BA, BG, HR, CY, GR, IT, PT, RO, UA	12	Citrus, Camellia, Coffea, Mentha, Solanum	CAB-International (1986), Childers et al. (2003a), Childers et al. (2003b), Glavendekić et al. (2005), Manson (1967)
Brevipalpus russulus (Boisduval 1867)	A	Phytophagous	C & S America	1867, FR	BE, DE, FR, GB, GR, NL, PT, UA	J100	Cactaceae	Denmark (1978)

Family	Status	Regime	Native range	1st record	Invaded	Habitat	Hosts	References
Species				in Europe	countries			
Tenuipalpus caudatus (Dugès 1834)	A	Phytophagous	Tropical	Unknown	FR, GR, IT, PT	12, J100	Citrus	Manson (1967)
Tenuipalpus pacificus	А	Phytophagous	C&S	Unknown	DE, GB, NL,	J100	Orchids:	Denmark (1968), Glavendekić
Baker 1945 -			America		RO, RS		Phalaenopsis, etc	et al. (2005), Manson (1967)
Tetranychidae								
Eotetranychus lewisi	A	Phytophagous	C&S	1990, PT-	PT-MAD	I	Citrus, Carica	Carmona (1992)
(McGregor, 1943)			America	MAD				
Eotetranychus weldoni	A	Phytophagous	North	2004, RS	AL, MK, RS	Ι	Populus	Glavendekić et al. (2005)
(Ewing, 1913)			America					
Eurytetranychus admes	А	Phytophagous	North	1970, HU FR, HU	FR, HU	12	Coniferous	Bozai (1970), Migeon (2003)
Pritchard & Baker,			America					
1955								
Eurytetranychus	А	Phytophagous	Asia-	1974, HU	HU	Ŋ	Picea	Bozai (1974)
furcisetus Wainstein,			Temperate					
1956								
Eutetranychus banksi	А	Phytophagous	C&S	2001, ES	ES, PT	I	Citrus	Garcia et al. (2003)
(McGregor, 1914)			America					
Eutetranychus orientalis (Klein, 1936)	A	Phytophagous	Asia-Tropical	2001, ES	ES	Ι	Citrus	Garcia et al. (2003)
Oligonychus bicolor	A	Phytophagous	North	1972, IT	IT-SAR, IT-	12	Quercus robur,	Rigamonti and Lozzia (1999)
(Banks, 1894)			America?		SIC, IT, PT		Castanea	
Oligonychus ilicis	A	Phytophagous	Asia-	1985, IT	IT, NL	12	Azalea,	Rota and Biraghi (1987)
(McGregor, 1917)			Temperate				Rhododendron, Camelia	
Oligonychus laricis	A	Phytophagous	North	1964, PL	PL	12	Larix	Boczek (1964), Doboz et al.
Keeves, 1905			America	- 1				(1995)
Oligonychus perditus	А	Phytophagous	Asia-	1990, NL	NL	12	Juniperus	Vierbergen (1990)
Pritchard & Baker,			Temperate				chinensis	
1000								

Family	Status	Regime	Native range	1st record	Invaded	Habitat	Hosts	References
Species				in Europe	countries			
Oligonychus perseae	Y	Phytophagous	North	2004, ES	ES	11	Persea	Alcázar et al. (2005)
Abbatiello, 1976			MIICIICA				arrerocara	
Oligonychus pritchardi (McGregor, 1950)	A	Phytophagous	North America	1984, PL	PL	Ŋ	Quercus robur	Kropczynska (1984), Doboz et al. (1995)
Oligonychus punicae (Hirst, 1926)	A	Phytophagous	C & S America	1988, FR- COR	FR-COR	12	polyphagous: Quercus, Juglans, Eucalyptus	Bolland et al. (1998)
Panonychus citri	A	Phytophagous	Asia	1950, FR	AL, BG, ES,	11, 12	Citrus	Balevski (1967), Bernini
(McGregor, 1916)					ES-CAN, FI,			et al. (1995), Bowman
					FR, GB, GR-			and Bartlett (1978), Bozai
					CRE, GR,			(1970), Ciampolini and Rota
					HR, HU,			(1972), Ciglar and Barić
					IT, IT-SAR,			(1998), Delrio et al. (1979),
					IT-SIC, MK,			Emmanouel and Papadoulis
					NL, NO, PL,			(1987), Fauna Europaea
					PT, RO, SI,			(2009), Garcia Mari and de
					UA, YU			Rivero (1981), Jeppson et al.
								(1975), Mijušković (1953),
								Pande et al. (1989), Petanović
								(1980), Rambier (1958),
								Vacante (1983), Vappula
								(1965), Vierbergen (1989)
Petrobia (Tetranychina)	Y	Phytophagous	North	1968, GR	GR	I	Lupinus.,	Hatzinikolis (1970),
lupini (McGregor,			America				Fragaria,	Papaioannou-Souliotis et al.
1950)							Poaceae	(1993)
Schizotetranychus	Y	Phytophagous	Asia-	2001, FR	FR	12	Bambusaceae	Auger and Migeon (2007),
bambusae Reck, 1941			Temperate					Migeon et al. (2004)
Schizotetranychus	А	Phytophagous	North	1964, PL	PL	\vdash	Cynodon,	Boczek and Kropczynska
parasemus Pritchard & Baker 1955			America				Poaceae	(1964)
Danci, 1777								

Family	Status	Regime	Native range	1st record	Invaded	Habitat	Hosts	References
Species				in Europe	countries			
Stigmaeopsis celarius	A	Phytophagous	Asia-	1985, FR	BE, FR, GB,	I, X11, X22,	Bambusaceae	Auger and Migeon (2007),
Danks, 1917			remperate			723, 724, 72)		Starzewski (2000), Witters et al. (2003)
Tetranychus canadensis (McGregor, 1950)	A	Phytophagous	North America	1954, HU	HU, PL	12	Polyphagous: Rosaceae,	Boczek and Kropczynska (1964), Hetenyi (1954)
Tetranychus evansi Baker & Pritchard, 1960	A	Phytophagous	C & S America	1991, PT	ES, ES-BAL, ES-CAN, FR, IT, PT, PT- MAD, PT	I, J100, X	Solanaceae	Castagnoli et al. (2006), Ferragut and Escudero (1999), Ferragut et al. (1997), Ferreira and Carmona (1995), Migeon (2005) Migeon (2007)
Tetranychus kanzawai Kishida, 1927	A	Phytophagous	Asia-Tropical	1966, GR	BE, GR	J100	Saxifragaceae: Hydrangea	Hance et al. 1998, Hatzinikolis (1968), Hatzinikolis (1986)
Tetranychus macfarlanei Baker & Pritchard, 1960	A	Phytophagous	Asia-Tropical	1989, ES- CAN	ES, ES-CAN	Ι	Musa, Ipomoea, etc	Pande et al. (1989)
Tetranychus mcdanieli McGregor, 1931	A	Phytophagous	North America	1981, FR	FR	П	Vitis, Acer, Lonicera, Fragaria, Ulmus, etc.	Rambier (1982)
Tetranychus neocaledonicus André, 1933	A	Phytophagous	Tropical	1989, ES- CAN	ES-CAN	П	Polyphagous: Citrus, Fabaceae	Ferragut and Santonja (1989)
Tetranychus sinhai Baker, 1962	A	Phytophagous	North America	1964, PL	PL	Ι	Heliantbus, Agropyron, Prunus	Boczek (1964)
Tetranychus tumidellus Pritchard & Baker, 1955	A	Phytophagous	North America	1986, GR	GR	Ι	Sambucus, Passiflora, Solanum	Hatzinikolis (1986)

Family Species	Status	Regime	Native range 1st record in Europe	1st record in Europe	Invaded countries	Habitat	Hosts	References
Tetranychus yusti McGregor, 1955	A	Phytophagous	C & S America	1981, GR	1981, GR GR, GR-CRE	12, X	Plumeria, Lonicera, exotic Fabaceae	Hatzinikolis (1986)
Varroidae								
Varroa destructor Anderson & Trueman, 2000	A	parasitic/predator	Asia	1964 RS	AL, AU, BG, CH, CZ, DE, DK, EE, ES, FI, FR, FR- COR, GB, GR, HU, IE, IT, IT-SAR, IT-SIC, LU, MT, NL, PL, PT, RO, RS, RU, SI, SK	J	bee parasite	Colin (1982), De Rycke et al. (2002), Griffiths and Bowman (1981), Morse and Goncalves (1979), Ruttner (1983), Ruttner and Marx (1984)

Table 7.4.2. List and characteristics of the mite species alien in Europe. Country codes abbreviations refer to ISO 3166 (see Appendix I). Habitat abbreviations refer to EUNIS (see Appendix II).

Argasidae Argas reflexus (Fabricius, 1794) pred Eriophyidae Aceria albestris Phy)	in Europe	myaueu counties	Habitat [↑]	Hosts	References
794)							
	parasitic/ predator	Europe	19th , DE	AT, BE, BG, CH, CZ, DE, DK, ES, FR, GB, GR, IT,	J	Rat	Dautel and Kahl (1999)
35				PL, RO, RU, UA			
	Phytophagous Alps	Alps	1952, CZ	1952, CZ AT, CZ, IT, RS	F2	Rododendron ferrugineum	Petanović and Stanković (1999)
Aceria loewi (Nalepa, 1890)	Phytophagous	Mediterranean East	1901, RO	AT, BG, CZ, CY, DE, FR, HU, IT, LT, LV, PL, GB	I2, X11	Syringa	Fauna Europaea (2009)
Aculus hippocastani Phy (Fockeu, 1890)	Phytophagous	Mediterranean East	1907, CZ	BG, CZ, IT, RO, FR	G1,G4, X11	Aesculus	Fauna Italia
Eriophyes canestrinii Phy (Nalepa, 1891)	Phytophagous	Mediterranean region	1998, RS	AT, BG, CZ, DE, HU, IS, PL	X 11, X24	Buxus sempervirens	Petanović (1998)
Glycyphagidae							
nesticus)	detrivorous	Europe	Unknown	DK, FÖ, IT, NO, J1, J2 PL, SE	J1, J2	Houes dust	Bigliocchi and Maroli (1995), Hughes (1976), Musken et al. (2000), Piotrowski (1990), Razowski (1997), Thind and Clarke (2001)
Ixodidae							
Hyalomma scupense par. Delpy 1946 pree	parasitic/ predator	Europe	Unknown	AL, BG, ES, ES-CAN, FR, GR, HR, IT, IT-SAR, IT-SIC, MK, RU, RS, YU	J	Cattle	Morel et al. (1977)

Family Species	Regime	Native range	1st record in Europe	1st record Invaded countries in Europe	Habitat*	Hosts	References
Rhipicephalus sanguineus parasitic/ (Latreille 1806) predator	parasitic/ predator	Mediterranean region		BE, CH, CZ, DE, DK, GB, IE, NL, NO, PL	ſ	Dogs	Černý (1985), Fauna Europaea (2009), Garben et al. (1980), Sibomana et al. (1986)
Phytoptidae							
Trisetacus laricis ((Tubeuf 1897)	Phytophagous Alps	Alps	1912	BA,DE, GB, HR, 12 SI	12	Larix	Fauna Europaea (2009)
Phytoseiidae							
Ambhyseius (Iphesius) degenerans (Berlese 1889)	parasitic/ predator	Mediterranean 1993, CZ CZ, GB, GR, IT,PT	1993, CZ	CZ, GB, GR, IT,PT	I	Predator of Tetranychus	Predator of Albajes et al. (1999), Bartlett (1992), Tetranychus EPPO (2002), Šefrová and Laštůvka (2005), Sengonca et al. (2004), van Houten and van Stratum (1993), van Houten and van Stratum (1995)